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Experience drives the development of movement-cognition correlations in a butterfly

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Correlations between behavioral traits are widespread, but the developmental genetic architecture of such correlations is poorly characterized. Understanding the developmental mechanisms that lead to correlations between behaviors has implications for predicting how changing environments might alter the strength, direction and persistence of these associations. Here we test the idea that genetic variation in one behavioral trait can drive the development of traits related to a second behavior, resulting in correlations between them. We focus on correlations between movement and aspects of cognition, in particular accuracy of decision making and neural investment. Such syndromes have been seen across a variety of systems, from insects to birds, but the direction of the correlation often varies. We use cabbage white butterflies as a system because they are easy to rear in large numbers and show ample genetic variation in both movement and learning, facilitating a split-sibling design. We test the prediction that variation in established proxies for movement at emergence will be correlated with the development of cognitive traits later in life (in siblings). Our results suggest that genotypes (full-sibling groups) that emerge with more elongate wings explore their environment more rapidly. In addition, genotypes that emerge with relatively smaller thoraxes are more likely to learn to search for atypical host plants and subsequently develop larger brains and brain regions. Taken together, genotypes that invest less in flight are slower, better learners and develop larger brains. These data are consistent with the idea that movement can drive the development of other behavioral traits, resulting in the emergence of correlated behaviors.

Keywords: flight muscle, wing shape, brain size, cognition, personality

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Introduction

Correlations between movement and aspects of cognition are ubiquitous (Marchetti and Drent, 2000; Dugatkin and Alfieri, 2003; Sneddon, 2003; Bolhuis et al., 2004; Mery et al., 2007; Exnerova et al., 2010). In some studies, fast-moving, bold individuals are those with limited flexibility in behavior, poor long-term memory or smaller brains (Verbeek et al., 1994; Mery et al., 2007; Burns and Rodd, 2008; Exnerova et al., 2010). However, in other instances, there are positive correlations between movement and cognitive traits (Dugatkin and Alfieri, 2003; Sneddon, 2003; Guenther et al., 2014a). Understanding these correlations is important to predict patterns of coexistence and survival within species (Dall et al., 2004; Sih et al., 2004a; Bolnick et al., 2011). For instance, certain personality or movement types may be more likely to colonize

new environments, influencing metapopulation dynamics (Bishop and Riechert, 1990; Hanski et al., 2004; Cote et al., 2010). Variation in movement and dispersal can also affect how organisms track environmental change (Higgins and Richardson, 1999; Thomas et al., 2001; Kotiaho et al., 2005; Poyry et al., 2009). However, how this variation in movement is correlated with cognitive abilities may affect whether a colonizing genotype survives in a new environment (Sol et al., 2002, 2005a). For instance, negative movement-cognition syndromes suggest that individuals most likely to colonize a novel environment may be the least likely to learn to use new resources in that environment.

While movement-cognition correlations have been documented across a range of systems, the developmental genetic architecture of these syndromes is unclear (**Figure 1**; Duckworth, 2010; Stamps and Groothuis, 2010a,b). Dissecting such proximate questions about behavioral syndromes is key to understanding how these correlations may break down or persist in the face of environmental or genetic change (Sih et al., 2004b). There are several proximate mechanisms by which correlations between behaviors might arise. In a handful of cases, correlated suites of behavior may stem from a set of genetic variants that are linked physically (e.g., in the same chromosomal region) or at the population-level due to mating patterns (e.g., "anxiety" traits in mice, Henderson et al., 2004). More commonly, behavioral syndromes emerge from pleiotropic effects of one or two genes as in the case of the foraging gene and rover-sitter *Drosophila* (Ben-Shahar et al., 2002; Mery et al., 2007). An idea receiving increasing attention in the literature is that of a niche-picking or niche-construction view in behavioral development (Stamps and Groothuis, 2010a; Stotz, 2010; Saltz and Nuzhdin, 2014). Exposure to different environmental conditions, such as enriched environments, high predation conditions or social stress, can influence the development of behavioral syndromes (Dirienzo et al., 2012; Edenbrow and Croft, 2013; Bengston et al., 2014). Thus, any genetic variation in traits that affect how an individual experiences the environment can result in genetic variation in behavioral syndromes. For instance, genetic variation in social preference has the potential to influence the development of personalities through the effects on a constructed social niche (Saltz, 2011; Montiglio et al., 2013).

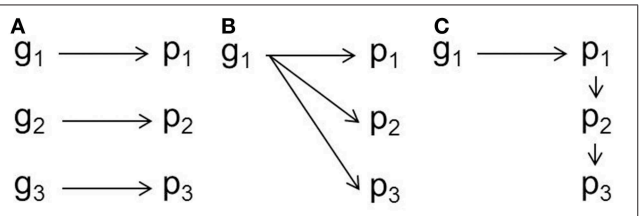

FIGURE 1 | Schematic of developmental genetic mechanisms underlying behavioral syndromes. (A) Linked genes (g) are associated with three correlated phenotypes (p). **(B)** One gene has pleiotropic effects on three phenotypes. **(C)** One gene affects one trait, which affects the development of other phenotypes, resulting in correlated traits. This latter mechanism, the focus of this research, would be considered a special case of "developmental" pleiotropy.

In this work, we focus on the hypothesis that genetic variation in movement-related traits affects the development of movement-cognition syndromes. It is well known that sensory stimulation during development can affect neural and behavioral development: exposure to enriched environments in development, (e.g., more social interactions or a range of resources), can result in neurogenesis, synaptogenesis and increased learning abilities (Van Praag et al., 2000; Arai and Feig, 2011). In more natural settings, an increase in sensory stimulation could stem from movement through different habitats, exposure to a range of resources or a combination of the two. Indeed, both movement and exercise have significant impacts on neural development (Olson et al., 2006). Taken together, these observations suggest that movement-cognition syndromes could emerge out of developmental interactions as organisms move through and interact with their environment.

Here, we test the hypothesis that slow exploration of the environment can affect the development of cognitive abilities, thus resulting in movement-cognition syndromes in adults. The decision-making literature suggests that there are often tradeoffs between the speed and accuracy of a decision (Dickman and Meyer, 1988; Chittka et al., 2009) which likely stems from limited attention and neural processing abilities (Bernays, 2001; Dukas, 2002). Such tradeoffs are thought to explain instances where fast, bold individuals are less flexible in the face of environmental change or invest less in neural machinery (Burns and Rodd, 2008; Sih and Del Giudice, 2012). In particular, it has been suggested that many syndromes may lie on a proactive-reactive axis, where bold individuals are where bold individuals are proactive. Bold individuals quickly explore and learn in a new environment but are less sensitive to new information and less capable of adjusting their behavior to environmental change (Sih....) (Sih and Del Giudice, 2012). We predict that such correlations emerge partly out of developmental interactions: slower exploratory movements earlier in development may drive the development of greater cognitive abilities, resulting in negative movement-cognition syndromes.

Dissecting the developmental basis of behavioral syndromes is challenging because measuring a trait at one time point may prevent or bias the measurement of that trait at a later time point. Family- or sibling-level approaches are one way around this problem which can simultaneously provide data on genetic variation in suites of correlated traits (Stamps and Groothuis, 2010a). In this study, we use a family-level approach to take independent measurements on naïve individuals sacrificed early in adulthood while their siblings, which were exposed to one of several behavioral assays, were tested at a later time point. We use the cabbage white butterfly, *Pieris rapae*, as a study system because they are easy to rear in common garden conditions, facilitating family-level designs (Snell-Rood and Papaj, 2009). In addition, we know learning affects resource use in many butterflies (Papaj, 1986a,b; Papaj and Prokopy, 1989; Weiss and Papaj, 2003), including *P. rapae*, which learn motor patterns for manipulating nectar resources (Lewis, 1986; Kandori and Ohsaki, 1996) and sensory cues associated with locating host plants or rewarding flowers (Traynier, 1984, 1986; Kandori and Ohsaki, 1996; Smallegange et al., 2006). In regards to host-searching behavior,

learning is particularly important for locating atypical red hosts (Snell-Rood and Papaj, 2009) and exposure to more difficult learning environments can have positive effects on neural development (Snell-Rood et al., 2009). In contrast, an innate bias to search for green colors minimizes the role of learning when typical, green-colored hosts are present. Overall, cabbage whites are an ideal system for testing how suites of cognitive traits are influenced by developmental experience.

In the present work, we make use of an existing experiment that tested for associations between genetic variation in host plant learning ability and neural investment (Snell-Rood et al., 2009). To the existing dataset, we have added several measurements, including search speed and two morphological proxies for movement. We primarily focus on relative thorax mass, which in butterflies is positively associated with investment in flight, in terms of acceleration and duration (Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004). We also focus on wing elongation, which is associated with greater acceleration, flight speed and distance (Betts and Wootton, 1988; Dudley, 1990; Berwaerts et al., 2002, 2008; Berwaerts and Van Dyck, 2004; Dockx, 2007). We relate measures of movement to measures of behavioral flexibility at different time points during adulthood. We test the primary prediction that if movement affects the development of cognition syndromes, movement traits at emergence will be related to cognitive traits (brain size and host-finding ability) assayed later in development, but not earlier in development.

Methods

Measures of Flight Capability

We used two morphological proxies for flight ability. First, we focused on thorax mass relative to body size, which has been linked to aspects of flight acceleration, speed and duration in over a dozen species of butterflies, including close relatives of *Pieris rapae* (Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004). For this measure, we used full siblings that had been sacrificed at emergence given that thorax mass changes over the lifespan of a butterfly (Stjernholm et al., 2005; Stjernholm and Karlsson, 2008; Snell-Rood et al., 2013). Individuals were stored frozen in glassine envelopes until measurement. Wings, head, abdomen and legs were removed from the thorax which was dried at 60°C in a drying oven for at least 24 h. Thoraxes were measured to the nearest 0.1 mg. We calculated the relative thorax mass of a family by running a model with family as a fixed effect and forewing area as a separate measure of body size. Least square means were taken from this model as our measure of size-corrected thoracic investment at emergence. Mean sample size per family was 5.2 individuals (range = 2–14).

Second, we used forewing "circularity" as a measure of forewing elongation. Wing elongation has been linked to acceleration, flight speed and flight distance in at least four butterfly species (Betts and Wootton, 1988; Dudley, 1990; Berwaerts et al., 2002, 2008; Berwaerts and Van Dyck, 2004; Dockx, 2007). To measure circularity, wings of individual butterflies were removed with forceps, photographed and measured in Image J (NIH). Circularity is a function of wing area and perimeter [4π(area/perimeter^2)], thus, larger values indicate a shape closer to a circle, less elongate. For family-level measures of wing elongation, we used individuals sacrificed at both emergence and after host-searching experience because experience did not affect the measurement, for instance through wing damage [$F_{(1,\ 341)} = 1.22$, $P = 0.27$]. Because area is a component of this measurement, we did not correct for size. Mean sample size per family was 10.0 (range = 3–24).

Host-Finding Behavior and Neural Investment

Full description and analysis of the behavioral experiment is presented in Snell-Rood et al. (2009). Briefly, after rearing in a common garden on artificial diet, naïve butterflies were sacrificed at emergence for measures of brain size while their siblings were subjected to one of four host-searching assays (**Figure 2**). Mated female butterflies searched for either a green host (kale) or a red host (photic stressed *Barbarea vulgaris*) in either a simple or complex environment (simple = 50% hosts and 1 non-host type; complex = 20% hosts and 4 non-host types). Female butterflies sample potential host plants through landings where they "taste" chemicals in the plants with their foretarsii (Hern et al., 1996). We recorded all landings made during host searching using Noldus software that included a time stamp for each individual observation. After opportunities to search for hosts over a 2-day period (about 1–2 h of experience per individual), females were sacrificed for subsequent measures of neural investment. This host-searching assay, in a large flight cage (4 × 4 × 2 m tall), was the first opportunity for females to fly for longer distances and extended periods of time – prior to this assay they were housed in smaller 60 × 60 × 60 cm mating cages.

For family-level measures of host-finding performance, we focused on the proportion of host-searching landings on hosts vs. non-hosts (arcsine-square root transformed for normality). We contrasted performance in two of the four search environments—the most "difficult" search environment (red host, complex non-host) and the simplest search environment (green host, simple non-host). "Difficulty" was assessed based on performance (host-finding efficiency) in these host-search environments: both host color and non-host complexity had independent effects on host-finding (see analyses in Snell-Rood and Papaj, 2009; Snell-Rood et al., 2009). For example, initial searching in the red host environment was close to finding hosts at random chance. Additionally, these two environments had the most pronounced differences among full-sibling groups in performance [e.g., red-complex, Family effect = $F_{(9,\ 22)} = 2.35$, $P = 0.04$]. We focused on naïve individuals with at least 20 landings during their first-host-searching test period. We binned landings into a "naïve" category, landings 1–10, and an "experienced" category, landings 11–20. We took the average performance values for siblings from a family, using only families with at least 2 individuals for a given category (range 2–5, mean = 3.4 and 2.7 individuals for red-complex and green-simple environments).

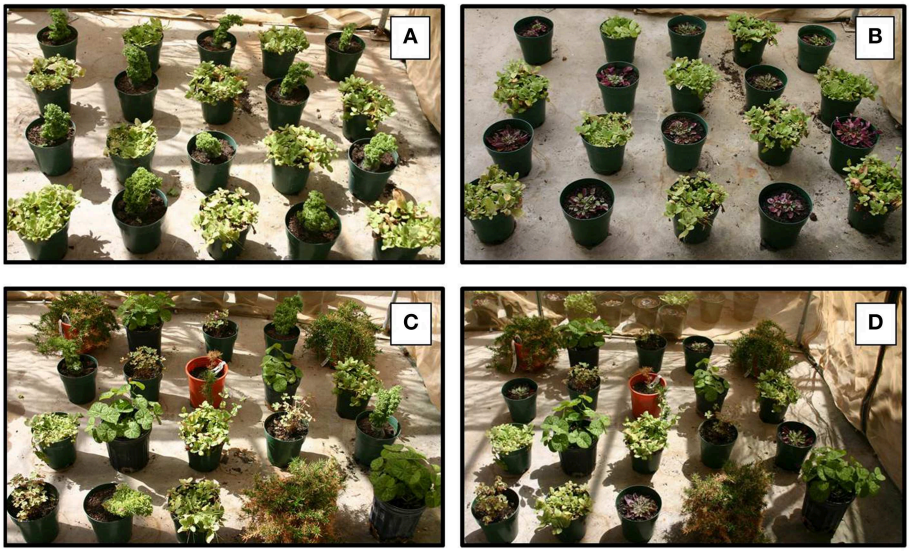

FIGURE 2 | Experimental setup. Individual female butterflies experienced environments that varied in host color (green vs. red color) or non-host complexity, which varied in diversity and density of non-hosts. **(A)** Green host, simple non-host environment. **(B)** Red host, simple non-host environment. **(C)** Green host, complex non-host environment. **(D)** Red host, complex non-host environment.

For measures of search speed, we focused on the median time between host-search landings (in seconds). It is important to note that during this time measurement, female butterflies are visually inspecting plants prior to landing on them and chemically gathering information with foretarsi after landing on them (rev. Hern et al., 1996). Thus, our measure of search time combines two types of exploration into one value. We take time flying between plants and time in contact with plants as one measurement of exploration time. This measure showed significant variation among full-sibling groups for initial landings in a model that controlled for search environment [landings 1–10: Family, $F_{(11,\ 183)} = 2.11$, $P = 0.02$, host color, $P = 0.004$, NH complexity, $P = 0.97$]. For later landings, time variation across families was not significant [landings 11–20: Family, $F_{(11,\ 110)} = 0.55$, $P = 0.86$, host color, $P = 0.02$, NH complexity, $P = 0.16$], but we still analyzed this variable as a contrast between time periods (consistent with our brain and performance measures).

This measure of exploration time focused only on landings butterflies made during active host searching. We focus on active host-searching because these behaviors are presumably the most relevant for fitness. However, we also considered time spent in other activities such as time spent sitting on plants and total search time (which includes time spent trying to escape and time flying around other parts of the flight cage). Time spent sitting on plants and total search time were not related to family variation in thorax mass [sitting time: $F_{(1,\ 9)} = 0.16$, $P = 0.70$; total flight time: $F_{(1,\ 9)} = 0.59$, $P = 0.46$].

A complete description of neural methods and analyses can be found in Snell-Rood et al. (2009). Briefly, butterfly heads were fixed in formalin and stored in cacodylate buffer until dissection. They were stained with osmium, embedded in plastic and sectioned at 15 microns. The volume of each brain region was measured using Image J (NIH). We focused on family-specific estimates of the total brain (from a model that corrected for body size using hindwing area) and the volume of individual brain regions (from a model that corrected for total brain volume). For specific brain regions, we only focused on those that showed family-level variation of experienced individuals (see Table 6, Snell-Rood et al., 2009), the central body, antennal lobes and medulla (part of the optic lobe). Measures of experienced brain size came from models that controlled for specific host-searching experience (host color, non-host complexity and total landings of an individual, $N = 49$ individuals from 7 families).

All statistical tests focused on family-level measures (i.e., each data point is a full-sibling family). Analyses were performed in JMP 9.0 (SAS Institute).

Results

There was significant variation across full-sibling families in both forewing circularity and thorax mass relative to body size [forewing circularity: Family: $F_{(11,\ 114)} = 4.84$, $P < 0.0001$; thorax mass: Family: $F_{(10,\ 41)} = 19.2$, $P < 0.0001$, forewing area: $F_{(1,\ 41)} = 70.9$, $b_{ST} = 0.02$, $P < 0.0001$]. These two proxies for movement were not significantly correlated (Spearman's $\rho = -0.07$, $P = 0.83$).

Butterfly families with more circular wings (less dispersive) were initially slower (i.e., had longer exploration times between host landings) during host search than those with more elongate wings [**Figure 3**; landings 1–10, $F_{(1,\ 10)} = 6.33$, $P = 0.03$]. However, this trend reversed, in a marginally significant manner, later during host search [**Figure 3**; landings 11–20, $F_{(1,\ 10)} = 3.84$, $P = 0.08$]. There were no significant relationships between search speed and thorax mass at emergence [landings 1–10, $F_{(1,\ 9)} = 0.54$, $P = 0.47$; landings 11–20: $F_{(1,\ 9)} = 0$, $P = 0.98$].

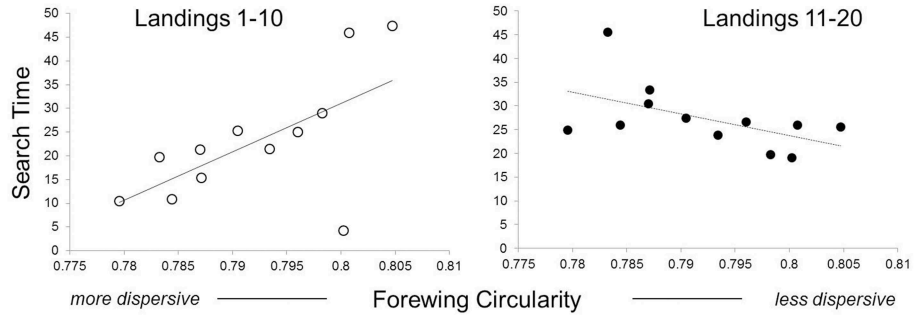

FIGURE 3 | Effects of wing elongation on speed of host-searching. Each data point represents a full-sibling family. Families with more elongate (less circular) wings spent less time initially searching their host environment. Search time is measured as the median time between host-searching landings (in seconds) for a given butterfly family. The left panel shows behavior of naïve individuals (first 10 host-searching landings) while the right panel shows behavior of experienced individuals (second 10 host-searching landings).

TABLE 1 | Associations between thorax mass at emergence and host-finding efficiency.

	Naïve individuals (landings 1–10)	Experienced individuals (landings 11–20)
Difficult search	$F_{(1, 7)} = 1.75$, $P = 0.23$, $b_{ST} = -!\,12.2$	$F_{(1, 7)} = 19.8$, $P = 0.003$, $b_{ST} = -25.7$
Simple search	$F_{(1, 8)} = 3.04$, $P = 0.12$, $b_{ST} = -15.9$	$F_{(1, 8)} = 1.07$, $P = 0.33$, $b_{ST} = -10.1$

*Shown are results results of family-level regressions for relationships between thorax mass at emergence (independent variable) and host-finding ability (dependent variable). Host-finding ability (proportion of landings on hosts vs. non-hosts) was considered early in host searching (landings 1–10) and later in host searching (landings 11–20) on the first day of search for naïve females. Females searched in either a difficult or simple search environment, where host color (green vs. red) and non-host diversity and density varied (see **Figure 2**).*

Butterfly families that emerged with relatively greater thorax mass (more dispersive) had poorer performance in the more difficult host-searching environment, where butterflies searched for red hosts within a diverse and dense non-host environment. However, this relationship was not present for naïve butterflies—it emerged after host-search experience (**Table 1**, **Figure 4**) and remained significant following a Bonferroni correction for four comparisons. There was no relationship between thorax mass and family performance in the simple host-searching environment (**Table 1**). There were no significant relationships between forewing circularity and measures of host-finding performance, although there was a marginally significant positive relationship between forewing circularity and experienced performance (landings 11–20) in the green host, simple non-host environment (**Table 2**).

Butterfly families that emerged with relatively greater thorax mass had smaller brains and brain regions, but only for measurements performed on experienced individuals (**Table 3**, **Figure 5**). More specifically, sibling groups with relatively smaller thoraxes had greater total brain volume along with regions of the brain dedicated to the antennal lobes and the central bodies. However, this relationship was specific to brain measurements of experienced individuals, not naïve individuals, although there was a marginally significant relationship between total naïve brain volume and relative thorax volume (**Table 3**). Two of these relationships (antennal lobe and whole brain) remained significant after a Bonferroni correction that accounted for four brain regions, but not when accounting for all eight comparisons. There were no significant associations between forewing shape and neural measures (**Table 4**).

Discussion

Genetic Variation in Movement Drives Emergence of Behavioral Correlations

Our results support the hypothesis that genetic variation in traits related to movement and exploration of the environment can drive the development of behavioral syndromes. Across all described patterns, variation in movement traits at emergence was tied to cognitive traits, but only those behavioral traits measured in experienced individuals, not naïve individuals. We focused on two validated proxies for movement that differed significantly between full-sibling groups of cabbage white butterflies. Previous studies have found that butterflies with a larger relative thorax mass and more elongate wings fly faster and further (Betts and Wootton, 1988; Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004; Dockx, 2007).

In the present study, we found three general patterns linking movement traits to behavioral traits. The first pattern suggests that individuals with different movement traits have different sampling strategies. Naïve females from families with more elongate (less circular) wings, explored their environment more rapidly when first searching for host plants (**Figure 3**). This suggests that more dispersive families explored visual and chemical plant cues less thoroughly than less dispersive families.

To evaluate whether these differences in movement might lead to the development of different aspects of cognition, we

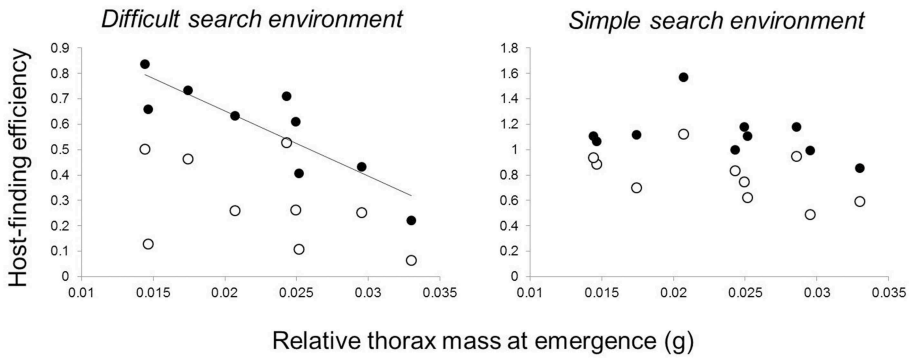

FIGURE 4 | Effects of relative thorax mass on host-finding efficiency. Each data point represents a full-sibling family. Host-finding efficiency (the proportion of searching landings on hosts vs. non-hosts, arcsine-square-root transformed) tended to increase between naïve butterflies (open circles—first 10 landings of a completely naïve host search) and later experience (closed circles—second 10 landings in the same searching sequence). Butterflies searched in either a difficult searching environment, where a red-colored host was interspersed amongst a high density of four non-host types, or a simple search environment where a green-colored host was interspersed in a low density of one non-host type.

TABLE 2 | Associations between forewing circularity and host-finding efficiency.

	Naïve individuals (landings 1–10)	Experienced individuals (landings 11–20)
Difficult search	$F_{(1, 7)} = 0.23$, $P = 0.64$, $b_{ST} = 3.94$	$F_{(1, 7)} = 0.60$, $P = 0.47$, $b_{ST} = 6.74$
Simple search	$F_{(1, 9)} = 0.46$, $P = 0.51$, $b_{ST} = 5.57$	$F_{(1, 9)} = 4.23$, $P = 0.07$, $b_{ST} = 13.7$

*Shown are results of family-level regressions testing for relationships between forewing circularity (larger values are less elongate wings) and host-finding ability. Host-finding ability (proportion of landings on hosts vs. non-hosts) was considered early in host searching (landings 1–10) and later in host searching (landings 11–20) on the first day of search for naïve females. Females searched in either a difficult or simple search environment, where host color (green vs. red) and non-host diversity and density varied (see **Figure 2**).*

TABLE 3 | Associations between neural investment and thorax mass.

	Naïve individuals	Experienced individuals
Antennal lobes	$F_{(1, 4)} = 0.01$, $P = 0.93$, $b_{ST} = 0$	$F_{(1, 5)} = 14.7$, $P = 0.01$, $b_{ST} = -0.11$
Medulla	$F_{(1, 4)} = 0.7$, $P = 0.45$, $b_{ST} = 0.31$	$F_{(1, 5)} = 3.2$, $P = 0.13$, $b_{ST} = 0.66$
Central body	$F_{(1, 4)} = 0.2$, $P = 0.68$, $b_{vST} = 0$	$F_{(1, 5)} = 11.7$, $P = 0.02$, $b_{ST} = -0.01$
Whole brain	$F_{(1, 4)} = 6.59$, $P = 0.06$, $b_{ST} = -3.15$	$F_{(1, 5)} = 14.9$, $P = 0.01$, $b_{ST} = -6.9$

Shown are results of family-level regressions testing for relationships between a family's relative thorax mass at emergence (independent variable) and measures of neural investment for siblings sacrificed at emergence or following host-searching activity. We only analyzed brain regions with significant family-level variation. Measures of individual brain regions account for body size variation.

tested whether movement traits and cognition were correlated in naïve and experienced individuals. In both cases, we found movement-cognition correlations only in experienced individuals. First, females from families with smaller relative thorax mass (less dispersive) were more capable of finding atypical host plants in complex environments (**Figure 4**), but this correlation was only evident in the second 10 host landings, after initial exploration of their environment. This result suggests that families with smaller relative thorax masses can more successfully learn to navigate complex environments than families with larger thoraxes. Second, butterflies from families with smaller thoraxes (less dispersive) were also more likely to develop larger brains (**Figure 5**) with larger regions involved in sensation (antennal lobes) and movement (central body, Strauss, 2002; Neuser et al., 2008). However, there were no correlations between movement traits and neural investment at emergence, consistent with the idea that initial variation in movement may have affected neural development.

Taken together, these data are consistent with the idea that variation between families in movement affects sampling strategy, the ability to find atypical resources, and, over developmental time, learning and neural development. Throughout, we have assumed that the differences between sibling groups reflect genetic variation. However, it is important to note that because we used a full-sibling design as opposed to a split-sibling design, it's possible that the family-level variation stems in part from maternal effects. Either mechanism is consistent with the idea that initial variation in behavior could drive the development of behavioral syndromes, but teasing apart genetic and maternal effects may give insights into how such syndromes might evolve as the environment changes. More specifically, genetic correlations between movement and cognition

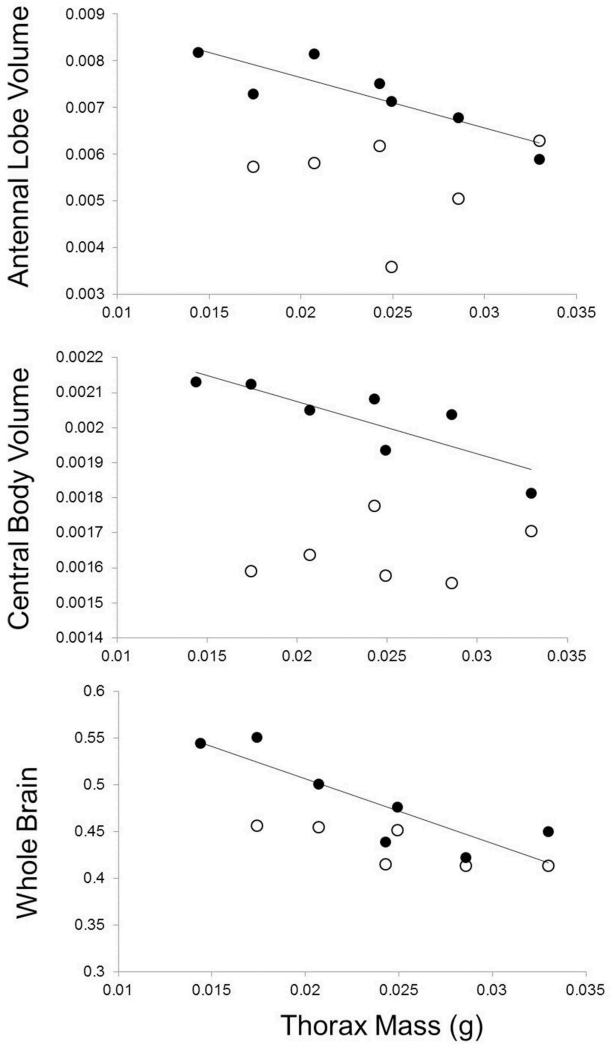

FIGURE 5 | Effects of relative thorax mass on neural investment. Full-sibling families with relatively smaller thorax mass at emergence developed larger brains and brain regions (experienced individuals shown with closed circles). There was no significant relationship between brain measures and thorax mass for brain measures taken on individuals sacrificed at emergence (open circles). Measures of individual brain regions account for body size variation.

that arise through gene-environment correlations have important evolutionary implications (Saltz and Nuzhdin, 2014). Niche-constructing behavior such as habitat preference or modification has the potential for generating complex evolutionary feedbacks because the selective environment potentially has a genetic component (Kerr and Feldman, 2003; Kylafis and Loreau, 2008). For instance, a decline in movement could decrease exposure to a range of environments, potentially weakening selection on learning and plasticity in certain environments (Sultan and Spencer, 2002; Scheiner et al., 2012). In some instances, by increasing the frequency of exposure to certain environments (e.g., atypical hosts), niche constructing behavior can speed up adaptation to those specific environments (Drown and Wade, 2014).

The present dataset is limited to only 12 full-sibling families. A more thorough quantitative genetic dissection of this question would consider a larger number of families. Such a design was not permissible in the present work which originally used behavioral measurements in four separate environments. However, we observed that the emergence of behavioral correlations was more pronounced in the most complex environment, similar to experiments in spiders which manipulated environmental enrichment (Bengston et al., 2014). These experiments suggest that the effects of niche construction and niche picking should be more pronounced in heterogeneous environments where behavioral variation would have more pronounced effects. From an experimental perspective, this suggests that limiting observations to one, complex environment would permit an increase in the number of families sampled, ideally using a split-sibling design to estimate maternal effects. Regardless, the limited family-level sample size for some of our comparisons (e.g., brain measures in **Tables 3, 4**) suggests that some of these comparisons should be treated as preliminary, informing follow-up studies.

We chose our proxies for movement based on existing research on butterfly flight patterns in over a dozen species, including those closely related to cabbage white butterflies (see citations above). Existing flight studies have considered butterflies in flight tunnels, tethered individuals or longer-distance free flight of wild individuals. These test conditions are somewhat different from the flight cage used here. However, the fact that thorax mass and wing shape tend to be important in a variety of experimental assays suggest they are also relevant for our assay. Additionally, while we were focused on short-distance flight patterns here, female cabbage whites move large distances in host-searching, sometimes 500–1000 m or more, spreading hundreds of eggs across many different host plants (Jones, 1977; Suzuki, 1978; Jones et al., 1980; Root and Kareiva, 1984). While it is likely these proxies for movement apply to host-searching in female cabbage whites, it's important that future studies validate the present patterns with measures of flight behavior in the field.

Overall, our results support the idea that variation in movement between families may result in the development of movement-cognition syndromes. For both neural measures and host-finding performance, movement traits (at emergence) were correlated with cognitive traits in experienced, but not naïve, individuals. Given the importance of exercise and enriched environments in neural development (Van Praag et al., 2000; Olson et al., 2006), it is not surprising that variation in movement between families could affect the expression of correlations between movement and cognition. Indeed, the same complex non-host and red host environments used in this experiment were previously shown to have positive effects on neural development in these butterflies (Snell-Rood et al., 2009). These results more broadly suggest that initial variation in a behavioral trait may affect the development of other traits, resulting in correlated behavior.

Insights into Movement-Cognition Syndromes Across Species

Our results linking measures of movement and cognitive behavior recall other systems where bold or dispersive genotypes are

TABLE 4 | Associations between neural investment and forewing circularity.

	Naïve individuals	Experienced individuals
Antennal lobes	$F_{(1, 4)} = 6.76$, $P = 0.06$, $b_{ST} = -0.09$	$F_{(1, 5)} = 1.39$, $P = 0.29$, $b_{ST} = 0.05$
Medulla	$F_{(1, 4)} = 1.21$, $P = 0.33$, $b_{ST} = 0.24$	$F_{(1, 5)} = 0.34$, $P = 0.58$, $b_{ST} = -0.21$
Central body	$F_{(1, 4)} = 6.86$, $P = 0.06$, $b_{ST} = -0.007$	$F_{(1, 5)} = 0.19$, $P = 0.67$, $b_{ST} = 0.002$
Whole brain	$F_{(1, 4)} = 4.04$, $P = 0.11$, $b_{ST} = 1.82$	$F_{(1, 5)} = 0.87$, $P = 0.40$, $b_{ST} = 2.44$

Shown are results from family-level regressions testing for relationships between a family's forewing circularity (larger values are less elongate wings) and measures of neural investment for siblings sacrificed at emergence or following host-searching activity. We only analyzed brain regions with significant family-level variation. Measures of individual brain regions account for body size variation.

less behaviorally flexible. Such correlations within species have been seen in both birds and fish (Verbeek et al., 1994; Burns and Rodd, 2008; Exnerova et al., 2010; Guillette et al., 2011). Across species, similar correlations have been noted with respect to migratory birds—migratory species have smaller brains and are less behaviorally flexible than temperate residents that have to cope with drastic changes across seasons (Sol et al., 2005b). Similarly, resident species of parrots (relative to nomadic species) tend to explore their environment more thoroughly and carefully (Mettke-Hofmann et al., 2012). Negative movement-cognition syndromes have also been suggested within humans with respect to attention deficit hyperactivity disorder (Rosenthal and Allen, 1978; Biederman et al., 1991; Blickle, 1996; Furnham et al., 2009).

Across species, however, there are examples of both positive and negative movement-cognition syndromes (Verbeek et al., 1994; Dugatkin and Alfieri, 2003; Sneddon, 2003; Mery et al., 2007; Burns and Rodd, 2008; Exnerova et al., 2010; Guenther et al., 2014a). Taking a developmental niche construction perspective can help to clarify such variation. Increased movement and dispersal may increase the degree of environmental variation an individual experiences, increasing the benefits of behavioral plasticity and learning (Papaj, 1994; Scheiner, 2013). However, if individuals are choosing to interact with only a subset of resources or environments experienced during dispersal, they may actually be experiencing more stable, predictable conditions, which would favor the use of innate behavior. Indeed, our results hinted that more dispersive genotypes (more elongate wings) may do better with more typical, green hosts, for which these butterflies have an innate bias (**Table 2**).

Why might more dispersive individuals invest less in learning and cognition? It is possible that such negative correlations could result from a tradeoff between investment in costly neural tissue and flight muscle (Isler and Van Schaik, 2006; McGuire and Ratcliffe, 2011). However, because negative relationships between neural tissue and thorax mass were less pronounced or entirely absent at emergence suggests there may not be inherent tradeoffs. It is possible that less dispersive individuals are making the "best of a bad situation." Nutritionally stressed larvae, for instance those with poor nitrogen assimilation abilities or access to a poor diet, may emerge as smaller adults, less able to fly around extensively. This idea recalls observations from other systems that early life nutritional environment may affect the development of behavioral syndromes (Andersson and Hoglund, 2012). However, it seems unlikely this explanation can account for the present results. We controlled for body size in our analyses; despite this, there were no significant relationships between family body size (a reflection of larval nutrition) and relative thorax mass or wing circularity. This idea also suggests that thorax mass and wing elongation would be more tightly correlated. A third explanation for such negative relationships between movement and cognition may be coexistence of a continuum of strategies. While more dispersive genotypes are likely to find more typical hosts spread over a broad area, less dispersive genotypes should be more likely to utilize locally common, less typical hosts. Overall, the fitness of these two strategies may well end up being identical. Movement-cognition syndromes may represent an instance where behavioral types coexist as different strategies with different routes to comparable fitness (Wolf et al., 2007, 2008).

Conclusions

This work contributes to a growing literature investigating the development of behavioral syndromes. A large number of studies have considered stability of behavioral correlations across ontogeny (Petelle et al., 2013; Boulton et al., 2014; Guenther et al., 2014b), which can give some insight into developmental mechanisms. A replicate genotype or quantitative genetics approach can give more insight into the developmental genetic architecture underlying a suite of correlated behaviors (Stamps and Groothuis, 2010a). The present study adds empirical weight to the idea that genetic variation in behavior such as movement or exploration can affect the development of behavioral syndromes. Such niche construction can result in gene-environment correlations and complex evolutionary feedbacks (Laland et al., 1999; Saltz and Nuzhdin, 2014). Given that most behavior affects how organisms experience the environment, and thus the subsequent development of traits, it's likely that such developmental feedbacks between traits and the environment (**Figure 1**) are a more general phenomenon in personality development, something that has long been recognized by psychologists studying human personality traits (Scarr and McCartney, 1983; Rutter and Silberg, 2002; Caspi et al., 2005).

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